Spatial pattern of grazing pressure of red deer (*Cervus elaphus*) in Norway

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Preface

This study was conducted as part of the NFR-project “Natural and farmed habitat as a basis for production of red deer in Norway”.

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Abstract

The dramatic increase of the red deer (*Cervus elaphus*) harvest in Norway the recent decades have led to concerns of possible oversized populations, and negative density effects on animal life history traits have been documented. However, few studies have been done on the state of the plant community. Measurements of accumulated browsing on important winter forage were conducted in two municipalities in Sogn and Fjordane, both to get better data on red deer diet and also in order to suggest whether such surveys may be a useful addition to monitoring animal performance in red deer management. I further quantified and analyzed the spatial patterns of browsing frequency of the highly selected rowan (*Sorbus aucuparia*) compared to the less selected blueberry (*Vaccinium myrtillus*) and birch (*Betula* sp.). I tested whether there were spatial variations in browsing frequency on a given plant species related to administrative units, habitat features and directly to variation in local population density or habitat use. A high utilization of low quality forage would indicate high population density relative to plant resources. From foraging theory, I predicted little spatial variation in browsing frequency of the highly selected rowan, and more variation for the assumed lower quality blueberry and birch. Administrative units explained little of the spatial variations in browsing frequency on rowan, while aspect, habitat forest type and productivity were the most important among factors describing the habitat. Slope and distance from arable land had a small effect on browsing frequency on rowan. There were some variations in browsing frequency on blueberry related to “Hunting area”, while “Block” explained most of the selection of birch. Of the parameters describing the habitat, habitat forest type and productivity were important for explaining spatial variation in browsing pressure on blueberry. Birch browsing frequency was affected by habitat productivity and altitude. Selection of all three plant species was positively correlated with red deer area use as assessed from faeces counts. Only blueberry showed variations in browsing frequency between “Hunting areas” which was related to local density, and I therefore argue that studies of browsing pressure on blueberry may be a useful tool in red deer management. This result also suggests that local variation in red deer density is not only due to habitat quality differences, but to local variation in management. Many plant species in Sogn and Fjordane are today heavily browsed, and further studies should try linking browsing pressure to changes in the plant community in order to assess broader ecosystem impacts.

Contents

1 Introduction

The deer family (*Cervidae*) consists of 40 species (Gilbert et al. 2006). They are a variable and adaptable group, and are found almost anywhere throughout the world (Gilbert et al. 2006). Many deer populations of Europe and North America have increased dramatically in numbers over the last decades (Alverson et al. 1988, Clutton-Brock and Albon 1992, Côté et al. 2004, Milner et al. 2006). The increase is both due to increase in density and also dispersal and establishment of new populations (Milner et al. 2006). The dense populations lead to great implications for the animals themselves in terms of density dependent effects, and there is being paid increasing attention to how deer affect the surrounding ecosystem and human interests (Côté et al. 2004). Large mammalian herbivores can have strong direct and indirect effects on plant community composition and structure (Augustine and McNaughton 1998). By grazing, browsing, trampling, defecation and urination, large herbivores may alter species composition of plants and ecosystem processes (Hobbs 1996, Mysterud 2006). Overgrazing and damage to forestry and agriculture is a great concern in management of large herbivores (Mysterud 2006). Therefore, the long-term sustainability of the current situation with many high density populations has been questioned, partly because it remains unclear how high the grazing pressure is and what level of grazing pressure the plants can cope with.

In recent years, we have achieved a good understanding of how the sequential effects of increasing densities affect reproduction and survival in large vertebrates (Eberhardt 2002). With increasing density, usually the following sequence is observed: (1) increased juvenile mortality, (2) increased age of first reproduction, (3), reduction in reproductive rate of adult females, and finally (4) decreased adult survival. For herbivores above 50 kg, fecundity of young females rather than juvenile survival might be more sensitive to environmental stress (Gaillard et al. 2000). Body weight is a major determinant of reproductive performance and survival in ungulates (Langvatn et al. 1996), and studies have concluded that population increase in red deer (*Cervus elaphus*) has a negative impact on the body weight of red deer (Mysterud et al. 2001b). The reason of the reduced weight may be because ungulates tend to eat forage of a lower quality in high density populations (Freeland and Choquenot 1990). Female red deer need to reach a specific body weight before they can ovulate, resulting in an increased age of first reproduction caused by increasing density and reduced condition (Langvatn et al. 2004). In addition, red deer hinds conceive at a higher body weight in high density populations (Albon et al. 1983). Later born calves have less time to gain weight through spring- and summertime, and studies from Scotland have shown that they are more likely to die than earlier born calves (Guinness et al. 1978).

Grazing pressure can be defined in several ways, often it is given for an entire area as “animal demand per unit weight of forage at any instant” (Scarnecchia and Kothmann 1982). A useful field approach is to look at the grazing frequency, i.e., the proportion of individual plants eaten over a given time period (Holechek et al. 1999, Evju et al. 2006), which for a given plant species may be a result of population density, habitat selection and diet preference, in addition to the composition of the plant community. When a deer chooses forage, it has a hierarchy of possible decisions. This range from choosing the habitat to feed in, to choosing particular plant parts within a special specimen. Forage may vary in quantity, quality, species composition, and distribution both within and between natural habitats (Langvatn and Hanley 1993). These are important decisions since even small changes in forage quality can influence the body growth of cervids (White 1983), which again have influence on female fecundity and reproductive success, competitive ability in males and winter survival (Guinness et al. 1978, Gaillard et al. 1992, Hewison 1996, Mysterud et al. 2001b). The grazing pressure will increase as populations get bigger, but at a certain point the grazing pressure will increase predominantly for low quality forage, since selectivity decreases when forage is in short supply due to high population density (Mysterud 2006). A high utilization of low quality forage can therefore be an indication of a high population density compared to forage resources. A study of grazing (or browsing) frequency of plant species with differing quality as forage can be a useful approach in studying the condition of available forage as a whole.

The harvest of red deer in Norway has increased from about 1500 shot animals in 1960 to 32 632 in 2007 (Statistics Norway 2008). The county of Sogn and Fjordane alone had 10 539 shot animals in 2007, the highest number of the counties of Norway (Statistics Norway 2008). There are probably several factors that have contributed to the dramatic increase of the deer population in Norway, including climate, absence of large predators, changes in agriculture and forestry practice, and the creation of a more strict hunting law with focus on selective culling of animals of low reproductive value (calves and males). The density effects that have increased the red deer population size in Norway have been measured directly on the animals, i.e. decreased juvenile survival (Loison and Langvatn 1998, Loison et al. 1999), later ovulation and increased age of first reproduction (Langvatn et al. 2004), decreased body weight and early senescence in males (Mysterud et al. 2001b), but little have been done on the effects on the plant community.

Despite its importance as a game species there have been remarkably few studies on the diet in Norway (Ahlèn 1965, 1975), and diet of red deer is known to vary regionally (Gebert and Verheyden-Tixier 2001). Red deer are classified as mixed feeders but they largely avoid fibers whenever possible (Hofmann 1989). Based on rumen content analysis we know that the spring and summer diet consists of large amounts of forbs and grasses (Albon and Langvatn 1992). During the 1960's, snow tracking indicated that winter diet consists of more browse and heather (*Calluna vulgaris*) (Ahlèn 1965). The palatable rowan (*Sorbus aucuparia*), willow (*Salix* sp.), aspen (*Populus tremula*), Norway maple (*Acer platanoides*) and ash (*Fraxinus excelsior*) are known to be highly selected browse among wild ruminants in Scandinavia (Ahlèn 1975). The blueberry (*Vaccinium myrtillus*), cowberry (*Vaccinium vitis-idaea*) and juniper (*Juniperus communis*) are also important forage for the red deer during winter in Norway (Ahlèn 1965, 1975). However, these studies were performed before the recent 10 fold increase in harvest, indicative of a similar density increase, which may affect diet selection.

The aim of my thesis is to quantify the spatial pattern of browsing pressure of some selected winter forage plants (browse species) of red deer in Sogn and Fjordane, Norway at the end of winter, in order to suggest whether such surveys may be a useful addition to body mass monitoring of red deer populations. First, I present browsing frequency and availability of all species. I will then test whether there are spatial variations in browsing frequency on a given plant species that can be related to either variation in population density or habitat use. I therefore first tested whether the spatial variation in browsing frequency was related to (1) administrative units (municipal, block, hunting area) possibly reflecting local variation in density, (2) to relevant biological factors describing habitat (habitat description, habitat productivity, canopy cover, aspect, slope, altitude, distance from arable land and distance from the coast) and to (3) direct measures of red deer habitat use or density (Table 1).

I specifically tested the prediction of browsing frequency to be higher near arable land (H1), since it is well known that red deer use agricultural pastures to a large degree (Rivrud 2007). From foraging theory, I would expect highly selected plants to be eaten irrespective of density, while forage of lower nutritional value should be under a harder browsing pressure in high density (or high use) areas. Secondly, I will therefore test the hypothesis (H2) that spatial variations in browsing pressure reflecting gradients in local density (or habitat use) to differ among plants depending on the overall level of selectivity. I predict (H2A) generally high selection and little spatial variation for the assumed highly selected rowan, and some spatial variations for the assumed lower selected blueberry (H2B) and birch (H2C).

Table 1. Variables used in this study to investigate what determines the browsing frequency of different red deer forage species.

1. Administrative variables	2. Factors describing habitat	3. Direct indices of red deer density and use
Municipal (n=2)	Habitat description	Local density (deer shot per km^2)
Block (n=6)	Habitat productivity	No. of faeces per plot
Hunting area (n=23)	Canopy cover	
	Aspect	
	Slope	
	Altitude	
	Distance to coast	
	Distance to arable land	

2 Material and methods

2.1 Study area

The field work was conducted in the municipalities Flora and Gloppen in the county of Sogn and Fjordane in western Norway (Figure 1). Flora is a coastal municipality, while Gloppen is more of an inland municipality east of Flora. The topography is characterized with steep slopes, divided by narrow valleys and fiords, and it gets generally steeper inland. In Flora and Gloppen the forest is mostly dominated by either pine (*Pinus sylvestris*) or birch (*Betula* sp.), with undergrowth of juniper, blueberry, heather and different types of grasses and herbs. Planted Norway spruce (*Picea abies*) stands are also found in the area, which is an important winter habitat for the red deer (Mysterud et al. 2001a). Agriculture is widespread in the flatter lowlands, and the arable land is mainly cultivated to pastures and meadows for grass production.

All average temperature and precipitation data mentioned here, based on mean values from the period 1961-1990, is achieved from three meteorological stations on Flora mainland and five in Gloppen (Institute of Meteorology 2007). Temperature and precipitation generally tends to decline from south to north and from coast to inland, while snow depth increases (Langvatn et al. 1996). The mean temperature varies from 1.6 °C in February to 13.4 °C in August on Flora mainland, and from -0.5 °C in February to 14.2 °C in July in Gloppen. The mean precipitation on the mainland Flora varies from 1985 mm/ya in Florø to 3520 mm/ya in Grøndalen, and from 1260 mm/ya in Sandane to 2760 mm/ya in Eimhjellen in Gloppen.

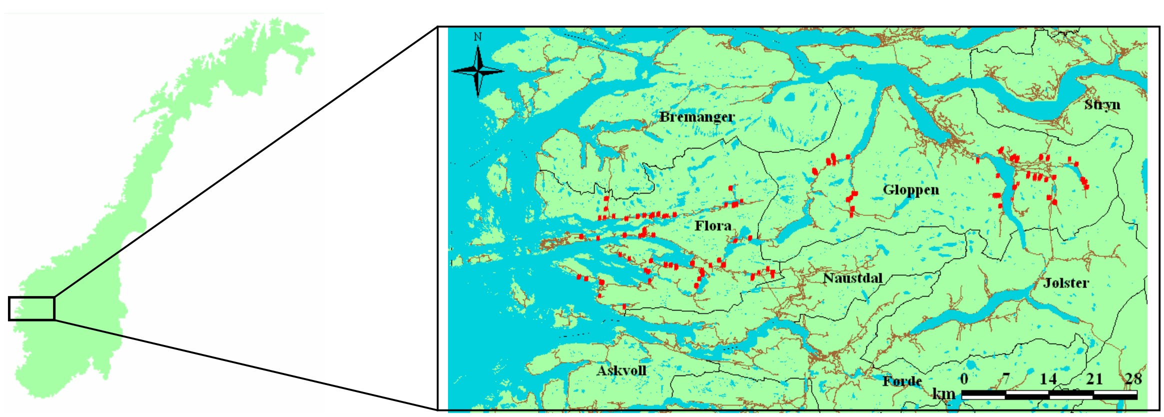

Figure 1. Map of the north-western part of Sogn and Fjordane, with the municipalities Flora and Gloppen centered. All transects carried out in this study is indicated by red markers.

2.2 Sampling and design

The field work was carried out over two seasons, from 10.04.2006 to 30.04.2006 in Gloppen and from 13.04.2007 to 03.05.2007 in Flora. Measurements are mainly of accumulated browsing over several years, so it is regarded of less importance that data derive from separate years in the two municipalities. A block-wise randomization sampling design with three blocks per municipal was used (Appendix 1). The block parameter will later be counted among the administrative units. First, a random block was chosen, then a random 1 km^2 square within the block, and then a random starting point of a transect. Each transect run from low to high altitude, with plots randomly distributed along the transect for every 20-50 m.

Every plot was a circle with a radius of 4 m (50.3 m^2), which is the standard protocol in forestry. For all specimens inside the plot area of pine, spruce, rowan, aspen and *Salix* sp., the number of browsed and unbrowsed shoots were counted. Concerning other tree species that were highly abundant and rarely browsed (Appendix 2), only a single tree nearest to the middle of the plot was examined. A 50x50 cm frame was placed over the blueberry nearest to the middle of the plot, and measurements of heather were carried out within this frame. Each transect was carried out until either 500 m above sea level or a hill top was reached, or until it was to difficult or dangerous to continue due to steep terrain.

Several relevant biological variables were measured and estimated in all measurement plots (Appendix 3). Slope and aspects were determined by using a Silva compass, and canopy cover by using a spherical densiometer, Model-C. All plots were registered with a GPS receiver (Garmin GPSMAP 60CSx). Availability was estimated based on whether or not available browse existed within the plots (i.e., plots with the species out of total number of plots).

2.3 Statistical analysis

All statistical analysis was run in the statistical software R vs. 2.5.1 (R Development Core Team 2007). Coordinates were plotted in ArcView GIS 3.3 (ESRI, Inc., Redlands, California), and distance from arable land, distance from the coast and habitat productivity was estimated. I used linear models to analyze variation in browsing frequency (i.e., number of browsed twigs from total number of twigs for a given plant). Browsing frequency was (arcsin-sqrt) transformed to obtain normality and to obtain residuals with constant variance. In the first model, all data was included with plant species as the single predictor variable. In the next step, I ran separate models for rowan, blueberry and birch, as these were the only species with sufficient data for such a comprehensive analysis. In the third step, I included variables of red deer density and the level of use. The best model was found through selection based on the AIC criterion (Appendix 4). I used a manual selection procedure, first focusing on only the administrative factors, then on biological factors describing the habitat, and at last on direct indices of red deer density and use (table 1). For the rowan analysis, the administrative unit hunting area was excluded from the model with only administrative factors because of strongly unevenly distributed data.

I used six habitat descriptions, consisting of 1) pine forest, 2) spruce forest, 3) deciduous forest, 4) mixed forest, 5) rocky ground and 6) marshland. The habitat categories of rocky ground, marshland and spruce forest were excluded from all analyses because of insufficient data in all analyses of spatial variation in browsing pressure. Digital maps, supplied by the Norwegian Forest and Landscape Institute were used to classify the habitat productivity. The non-productive classes 1, 2, 6 and 7 (agriculture, pastures, marshes, and mountains and bare land) were excluded. The remaining dataset included the habitat productivity classes 3-5: 3 = forest, very high productivity, 4 = forest, high productivity, 5 = forest, normal to low productivity. In all models of the blueberry analysis, five hunting areas (”Fossheim, Sandal og Torheim”, ”Kleppe, Støyva og Bjørnereim”, ”Midtbø”, ”Myklebust, Kobberstad” and ”Steindal, Svartdal, Osen”) were excluded because of lack of data points. Density was estimated by the number of red deer shot in the hunting season (10th of September to 15th of November) in the various hunting areas. Use was estimated by dung counts at each measuring plot.

3 Results

3.1 Browsing frequency and availability at the plant species level

There was large variation in browsing frequency of the different plant species (Figure 2). The model with only plant species as an explanatory variable explained 37% of the variation in browsing frequency. As expected from previous studies, the highly palatable aspen, rowan, and sallow (*Salix caprea*) and other willow were among the most frequently selected species. An unexpected finding was the high browsing frequency observed on bird cherry (*Prunus padus*) in some locations in the Gloppen municipality. Common plant species such as blueberry and birch were found to be intermediately selected species. Conifer tree species like pine, spruce and the shrub heather were among the least browsed species.

Blueberry is by far the most available species in Flora and Gloppen (Appendix 5). Birch and cowberry are also found fairly frequent. Heather, rowan and pine are among the plants with intermediate availability, while alder, bird cherry and willow have rather low availability. Hazel, moorberry, oak, spruce, aspen and holly are very little available. For the focal species (rowan, blueberry and birch), availability at the administrative unit "block" level was largely variable in both rowan and birch, but blueberry was more evenly distributed among blocks.

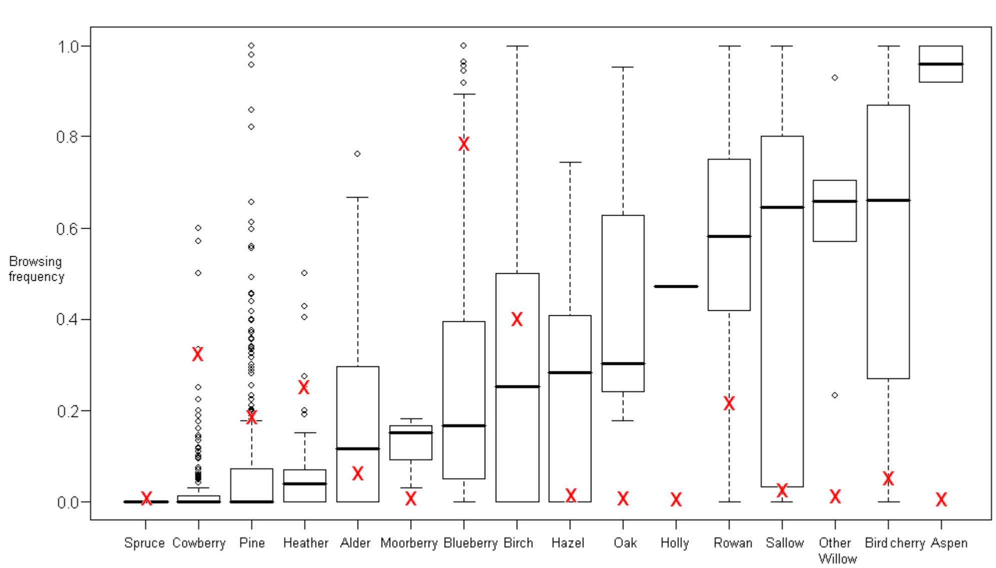

Figure 2. Overall red deer browsing frequency of the plant species encountered in the study area. Availability (whether or not available browse existed within a plot) is indicated by the red markers "X".

3.2 Spatial variation in browsing pressure

3.2.1 A highly selected species; the rowan

In the first part of the model selection with the administrative factors, the best model included only block (Table 2). When estimated, however, the difference between blocks was not significant, suggesting that for this highly selected species, there was little variation in browsing pressure between administrative units, as predicted from hypothesis H2A.

The best model, when including biological factors related to habitat, included aspect, habitat description, habitat productivity, distance from arable land, canopy cover and slope (Table 3). There was a higher selection of rowan in deciduous than in mixed forest (Figure 3). Pine forest was not significantly different from deciduous (estimate=0.051, p=0.417) or mixed forest (estimate=0.058, p=0.413). There was also a lower browsing frequency of rowan in productivity class 4 than in productivity class 3 and class 5 (estimate=0.139, p=0.015). Browsing in productivity class 3 and 5 were similar. The effect of distance from arable land was not significant when including all data points, but this result was heavily dependent on two outlying data points. When excluded from the analysis, there was a weak, but significant positive effect of distance from arable land on browsing frequency, i.e., contrary with hypothesis H1. Browsing of rowan decreased slightly with increasing slope. West facing slopes were significant less browsed than the other aspects, but east, north and south facing slopes were not significantly different. Cover, when estimated, was not significant. These results do suggest some spatial variation in rowan, which was not predicted from H2A.

In the third part of the model selection, which also included factors of red deer density and use, only the number of observed faeces was included. Faeces number was positively correlated with browsing frequency of rowan.

3.2.2 An intermediate selected species; the blueberry

The best model for administrative factors explaining spatial variations in browsing frequency of blueberry included hunting area (Table 2). As predicted from H2B, hunting area explained much of the variation in browsing pressure when estimated, showing variation on a very local scale.

In the model selection with biological factors describing the habitat, the best model included aspect, habitat description, habitat productivity, and distance from the coast (Table 3). Not in accordance with hypothesis H1, distance from arable land was not included in the best model based on factors describing the habitat. Browsing of blueberry was highest in mixed and deciduous forests, but with some degree of higher selection in mixed forests. Browsing frequency on blueberry was lowest in pine forest. Browsing in deciduous and mixed forest was similar, but with some higher browsing frequency in mixed forests. Browsing frequency of blueberry were different in deciduous and pine forest (estimate=0.134, p=0.011) (Figure 3). There was more browsing of blueberry in areas of productivity class 3 than in productivity class 4. Productivity class 5 was not significantly different from either class 3 or class 4 (estimate=0.046, p=0.426) when estimated. Distance from the coast did not have a significant effect on spatial variations in browsing frequency of blueberry. There was more browsing on blueberry in areas with south facing slopes, but aspect south was not significantly different from aspect north. East, north and west facing slopes were similar. Removal of outliers in the variable distance from arable land did not affect the best model.

The best model in the third part of the model selection with factors of red deer density and use, included both red deer density and number of observed faeces. Browsing frequency of blueberry increased with both density (figure 3) and number of faeces.

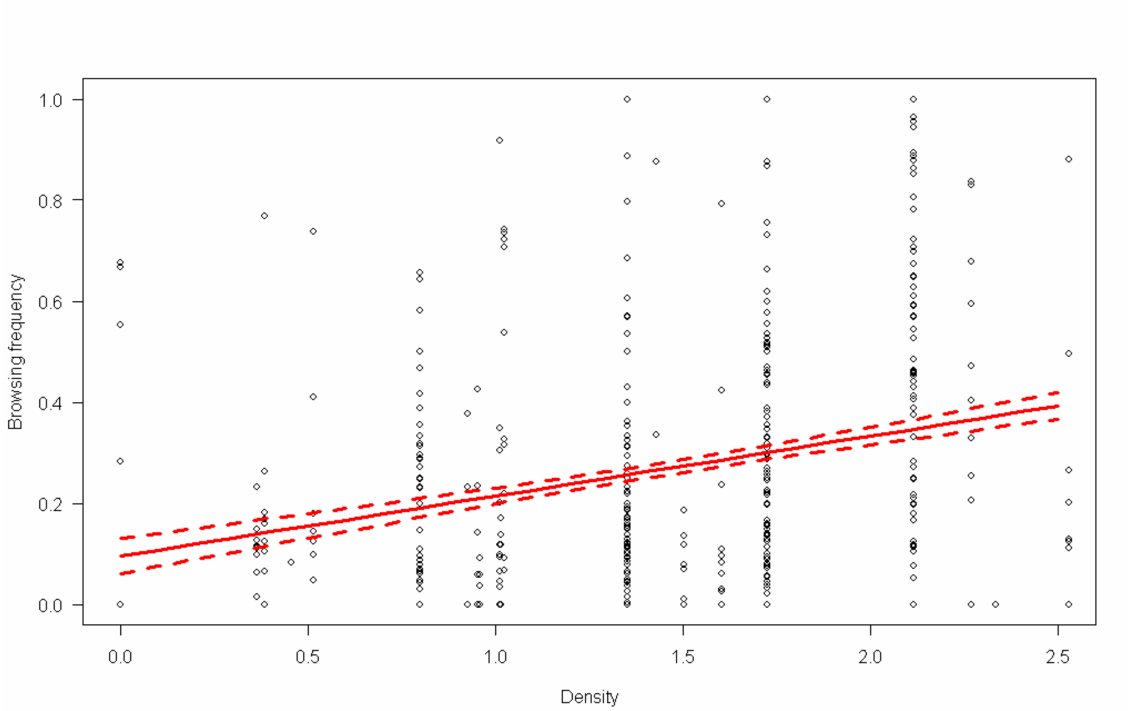

Figure 3. Plot showing the correlation between browsing frequency of blueberry and red deer density (No. deer harvested per km^2) at an administrative level (hunting area). Browsing frequency is at the plot level. The broken lines represent standard error limits.

3.2.3 An intermediate selected species; the birch

In the first part of the model selection with the administrative factors, the best model included block (Table 2). The blocks showed variation in browsing frequency of birch at the administrative level, as predicted from H2C.

The best model when including biologically relevant habitat factors for explaining spatial variations in browsing frequency of birch included productivity and altitude (Table 3). Contrary with hypothesis H1, distance from arable land was not included in the best model. The main pattern was highest browsing for birch in habitat class 4 and 5, and lowest browsing frequency in class 3 (Figure 3). Browsing levels in productivity class 4 and 5 were similar (estimate=0.057, p=0.444). Altitude had a weak negative effect on selection of birch, with continuously decreasing selection with increasing altitude (Table 3).

In the third part of the model selection, with factors of red deer density and use, only the number of observed faeces was included, and was positively correlated with browsing frequency of birch (Table 3).

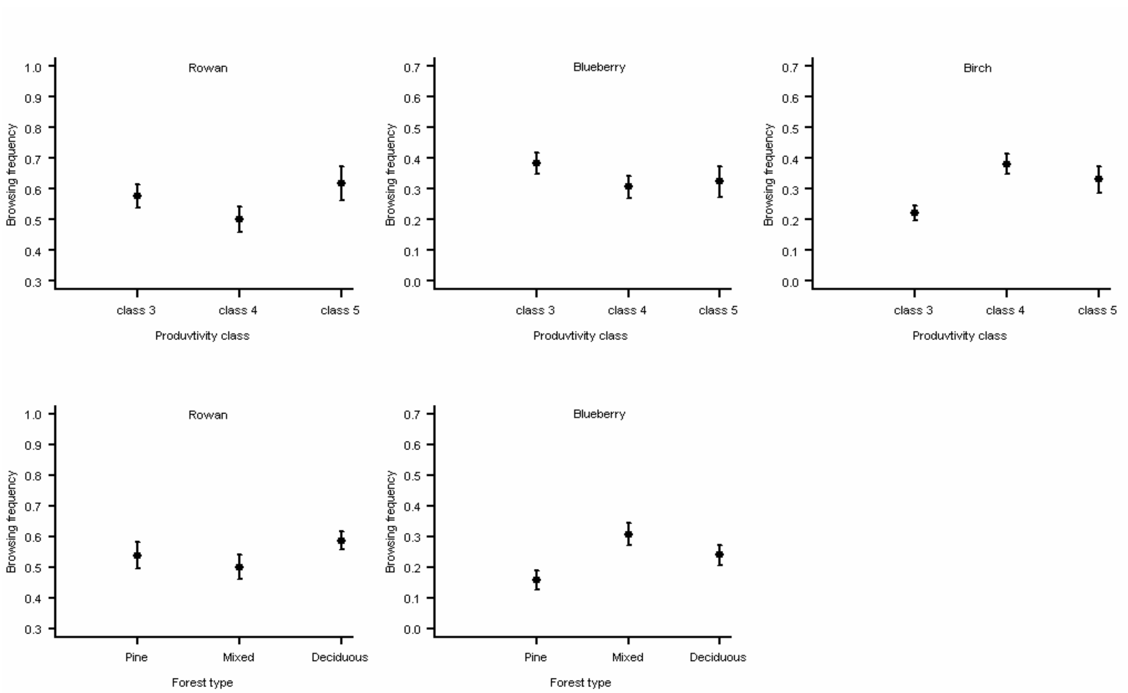

Figure 4. Browsing frequency of rowan, blueberry and birch related to habitat category-forest type (with regard to productivity class 4 and aspect north) and habitat productivity class (with regard to deciduous forest and aspect north). Productivity class 3-5 specify the different productivity classes; 3 = forest, very high productivity, 4 = forest, high productivity, 5 = forest, normal to low productivity.

Table 2. Parameter estimates from the best models explaining browsing frequency of red deer based on the AIC criterion when including only administrative variables (Table 1). Separate models were run for rowan, blueberry and birch. SE = Standard Error. CI = Confidence interval. * indicate p=0.05 statistical significance. Ha. = Hunting area. Bl.fjl.drp.= Blåfjellet Driftsplanområde.

Parameters	Estimate	SE	95% CI		
			Lower limit	Upper limit	
A. Rowan					
Intercept	0.836	0.159	0.525	1.148	*
Block (Byrkjelo vs. Breim)	-0.013	0.169	-0.345	0.320	
Block (Eikefjorden vs. Breim)	-0.008	0.163	-0.327	0.310	
Block (Hyen vs. Breim)	0.109	0.175	-0.233	0.452	
Block (Norddalsfjorden vs. Breim)	0.109	0.161	-0.206	0.424	
Block (Sunnfjord vs. Breim)	-0.028	0.169	-0.360	0.303	
B. Blueberry					
Intercept	0.684	0.049	0.589	0.78	*
Ha. (Dale og Kåle vs. Bl.fjl.drp.)	-0.684	0.156	-0.99	-0.379	*
Ha. (Eikefjord storvald vs. Bl.fjl.drp.)	-0.325	0.06	-0.443	-0.208	*
Ha. (Endestad vs. Bl.fjl.drp.)	-0.368	0.116	-0.595	-0.141	*
Ha. (Gjengedal vs. Bl.fjl.drp.)	0.042	0.108	-0.169	0.253	
Ha. (Gloppen Sør Viltlag vs. Bl.fjl.drp.)	-0.322	0.1	-0.518	-0.126	*
Ha. (Hetle - Reed - Fløtre vs. Bl.fjl.drp.)	0.087	0.081	-0.072	0.246	
Ha. (Hole, Moldestad og Felde vs. Bl.fjl.drp.)	-0.212	0.142	-0.491	0.066	
Ha. (Mjellem vs. Bl.fjl.drp.)	-0.176	0.123	-0.417	0.064	
Ha. (Norddalsfjord storvald vs. Bl.fjl.drp.)	-0.122	0.062	-0.243	-0.001	*
Ha. (Ommedal vs. Bl.fjl.drp.)	-0.077	0.118	-0.308	0.154	
Ha. (Skålefjell Hjortevald vs. Bl.fjl.drp.)	-0.373	0.101	-0.571	-0.176	*
Ha. (Stavøy vs. Bl.fjl.drp.)	-0.08	0.109	-0.294	0.133	
Ha. (Strømsnes vs. Bl.fjl.drp.)	-0.326	0.124	-0.569	-0.082	*
Ha. (Vasset ytre vs. Bl.fjl.drp.)	-0.484	0.129	-0.738	-0.23	*
Ha. (Vestre Hyen storvald vs. Bl.fjl.drp.)	-0.259	0.068	-0.392	-0.126	*
Ha. (Øvreset vs. Bl.fjl.drp.)	0.064	0.194	-0.315	0.444	
C. Birch					
Intercept	0.432	0.064	0.306	0.557	*
Block (Byrkjelo vs. Breim)	-0.126	0.078	-0.278	0.026	
Block (Eikefjorden vs. Breim)	0.283	0.092	0.103	0.463	*
Block (Hyen vs. Breim)	-0.072	0.082	-0.233	0.089	
Block (Norddalsfjorden vs. Breim)	0.411	0.089	0.237	0.585	*
Block (Sunnfjord vs. Breim)	0.154	0.090	-0.023	0.330	

Table 3. Parameter estimates from the best models explaining browsing frequency of red deer based on the AIC criterion when including only biological variables related to habitat (Table 1.). Separate models were run for rowan, blueberry and birch. SE = Standard Error. CI = Confidence interval. * indicate p=0.05 statistical significance.

Parameters	**Estimate**	**SE**	**95% CI**		
			Lower limit	**Upper limit**	
A. Rowan					
Intercept	0.886	0.076	0.737	1.035	*
Aspect (north vs. east)	-0.028	0.049	-0.123	0.068	
Aspect (south vs. east)	-0.029	0.063	-0.153	0.095	
Aspect (west vs. east)	-0.298	0.075	-0.445	-0.152	*
Forest type (Pine vs. Mixed)	0.058	0.070	-0.080	0.196	
Forest type (Deciduous vs. Mixed)	0.108	0.052	0.007	0.210	*
Productivity (class 4 vs. class 3)	-0.101	0.048	-0.195	-0.006	*
Productivity (class 5 vs. class 3)	0.038	0.067	-0.094	0.170	
Distance to arable land	0.000	0.000	0.000	0.000	*
Cover	0.002	0.001	0.000	0.004	
Slope	-0.004	0.002	-0.007	0.000	*
B. Blueberry					
Intercept	0.543	0.061	0.423	0.663	*
Aspect (north vs. east)	0.087	0.056	-0.023	0.197	
Aspect (south vs. east)	0.121	0.055	0.014	0.228	*
Aspect (west vs. east)	-0.009	0.076	-0.157	0.139	
Forest type (Pine vs. Mixed)	-0.216	0.049	-0.313	-0.12	*
Forest type (Deciduous vs. Mixed)	-0.082	0.046	-0.173	0.008	
Productivity (class 4 vs. class 3)	-0.099	0.041	-0.179	-0.019	*
Productivity (class 5 vs. class 3)	-0.053	0.06	-0.17	0.065	
Distance from coast	0	0	0	0	
C. Birch					
Intercept	0.657	0.058	0.544	0.770	*
Productivity (class 4 vs. class 3)	0.197	0.058	0.084	0.310	*
Productivity (class 5 vs. class 3)	0.140	0.067	0.009	0.270	*
Altitude	-0.001	0.000	-0.002	-0.001	*

Table 4. Parameter estimates from the best models, when including direct indices of red deer density and use, explaining browsing frequency of red deer based on the AIC criterion. Separate models were run for rowan, blueberry and birch. SE = Standard Error. CI = Confidence interval. * indicate p=0.05 statistical significance.

Parameters	**Estimate**	**SE**	**95% CI**		
			Lower limit	**Upper limit**	
A. Rowan					
Intercept	0.844	0.081	0.684	1.003	*
Area use	0.088	0.020	0.049	0.127	*
B. Blueberry					
Intercept	0.431	0.057	0.319	0.543	*
Density	124.075	30.005	65.266	182.884	*
Area use	0.023	0.010	0.005	0.042	*
C. Birch					
Intercept	0.640	0.058	0.527	0.753	*
Area use	0.027	0.013	0.002	0.053	*

4 Discussion

Of the many factors describing habitat features, habitat description and habitat productivity seem to be the most important variables of explaining spatial differences in browsing pressure, although aspect also may be important especially for rowan. Contrary with hypothesis H1, browsing pressure was not higher near arable land for any of the species. The little variation in browsing pressure between administrative units observed in rowan supports the prediction that this species is browsed more independently of red deer density (H2A), later confirmed since local red deer density did not enter in the last stage of model selection. Blueberry showed variation in browsing frequency between administrative units, supporting the hypothesis that browsing of this species in Gloppen and Flora reflects gradients in local deer density and/or habitat use (H2B). Confirming this hypothesis, density was seen to influence browsing frequency of blueberry when included. Birch showed spatial differences in browsing frequency between administrative units, but density was not included in the third step of model selection. This suggests that either variations in habitat use or spatial differences in forage quality may affect selection of birch, which may be related to a problem of within-species quality variation (see below).

4.1 Diet selection of red deer during winter

Diet selection is fundamental in understanding how herbivores interact with plant structure- and composition, and the ecological relations in the habitats (Hanley 1997, Augustine and McNaughton 1998). The deer first choose in which habitats to find their forage, and then select which individual plant species within the vegetation community, and even plant parts within specific specimens to feed upon. Because forage types differ greatly, and because ecological and evolutionary processes takes place on the species level, theory of diet selection concentrate on the plant species level (Hanley 1997). Digestible protein and energy are usually the two components of shortest supply to deer (Hanley 1997). How much nutrients and energy the animal needs depends on seasonal demands. During winter with little muscle growth, energy intake is usually regarded as the most critical factor in diet selection (Robbins 1993). Among the most important factors influencing diet selection in deer is digestion time (Hanley 1997), especially important in winter when high energy forage is generally rare. Studies have documented a positive correlation between highly selected and rapidly growing

(Bryant et al. 1989) and easily decomposable plants, since the same chemical properties that determine the decay of a plant also determine the digestibility (Pastor and Naiman 1992).

Herbaceous forage like forbs and grasses are commonly preferred by red deer (Albon and Langvatn 1992), since browse generally have a poor nutrient content, slow rate of breakdown and digestion, and high lignin-cutin concentrations (Robbins et al. 1987). Snow cover on the west coast of Norway will often limit the food supply of the red deer in wintertime, and as a consequence, the diet consists of more browse and different species of shrubs (Ahlèn 1965). Forbs and grasses are also mostly withered and dead at this time of year. Diet selection change under different conditions, and the accessibility of forage never remains constant (Hanley 1997). The utilization and importance of various species will differ greatly from region to region (Gebert and Verheyden-Tixier 2001), and the diet of red deer is seen to vary in different areas in Norway (Ahlèn 1965). The rowan, aspen and willow were among the most selected plant species in Flora and Gloppen. This was expected, but the high utilization of bird cherry came as a surprise. Norway maple and ash may also be important forage for the red deer in Norway (Ahlèn 1965, 1975), but these species were not encountered in this study. Bird cherry was found in 5.1 % of the measuring plots, all in Gloppen. Even if aspen and willow were heavily browsed, specimens with available browse (branches below 2 m) could only be found in respectively 0.4 and 3.0 % of the plots. Because of low abundance of available browse, bird cherry, willow and aspen are probably not important winter forage for the deer to any large extent. Rowan was found in 21.4 % of the plots, and may still, even if heavily browsed, be important winter forage for red deer populations in Flora and Gloppen. Pine were found in 18.2 % of the plots, but were in general not much browsed, even if it could be rather heavily browsed in a few areas. Alder was selected fairly low, and only found in 6.0 % of the plots. The birch was surprisingly heavily browsed. Birch was found in 40.2 % of the plots, and can be an important forage supplement for the red deer. However, I observed that the majority of this was due to browsed root shoots of birch (saplings), growing out of the stem basis of large birch trees, and the branches were not browsed to a considerable degree, but this was unfortunately not quantified. Blueberry was moderately browsed, while both heather and cowberry was slightly browsed, and even though they were found in 25.0 and 32.3 % of the plots, are probably not important forage for the red deer in these areas. Blueberry was found in 78.0 % of the measuring plots, with an average coverage of 10 % and height of 15 cm. Due to its distribution and abundance, blueberry is probably one of the most important winter forage species in wintertime for the red deer when snow depth is moderate. Observations made alongside this study seems to support that also juniper may play an important role as winter forage for red deer, as earlier observed (Ahlèn 1965). There were very few observations of bark gnawing in this study, and this does not seem to be a problem in Flora and Gloppen.

The functional responses of an animal are described as changes in intake rate as the result of changes in food abundance (Solomon 1949). Although the intention of this study was not to address functional responses, this may be an important part in understanding limitations in diet selection, habitat choice and social organization (Hanley 1982, Illiuis and Gordon 1990, Hanley 1997). Studies with large grazing herbivores have frequently shown a response fitted to the expected asymptotic type II functional response, while browsers feeding of forbs and shrubs have shown no responses to changes in plant biomass (Spalinger and Hobbs 1992). Tests have supported that competition between cropping and chewing are responsible for the type II functional response seen in herbivores feeding in food concentrated patches (Gross et al. 1993). From the composite model of Hobbs et al. (2003), the intake rate of an animal is seen to be regulated by plant density when the spacing between are above a certain threshold (animals can chew as they search for food), and by biting size when plants are spaced more closely together. However, researchers have asked for a more flexible explanation for functional response mechanisms, and the usage is frequently debated.

4.2 Spatial variation in browsing frequency

For a given plant species, spatial variation in browsing frequency can occur for several different reasons, for example forage selectivity (Mysterud 2006), spatial variations in plant phenology and local quality (Albon and Langvatn 1992, Mysterud et al. 2001a), plant community composition (Hester and Baillie 1998), by the attractions or tasty neighbors (i.e. other adjacent high quality of preferable resources) (Palmer et al. 2003), variations in habitat use (Palmer and Truscott 2003) and population density (Evju et al. 2006). There was little variation in browsing frequency of rowan between administrative units, but a more browsing of rowan was observed in very high productive and deciduous forest. Selection of rowan increased slightly with distance from arable land, but decreased with increasing slope, and browsing was lowest on west facing slopes. The administrative unit hunting area explained some of the distribution in browsing frequency in blueberry. Browsing of blueberry was highest in mixed and deciduous forest, and in areas of very high productivity. There was more browsing on blueberry in south facing areas. Block explained some of the variation of browsing frequency of birch. There was a trend of more browsing for birch in habitats with normal to low and high productivity and there was a slightly decreasing browsing frequency with increasing altitude. Because it is sometimes almost impossible to determine if a browsing incident is from during last winter or from previous years, this study measured accumulated browsing over several years. Faeces counts of pellet groups tells us something about red deer area use the last winter season, and was used to estimate habitat use on a small scale. When combined with browsing frequency, we will get a better picture of red deer browsing the previous year, since faeces tells us nothing of red deer habitat use in earlier years (all faeces from these years are decomposed and gone). Animals shot in the hunting season 2006 made the basis for density estimations (at the hunting area level). Selection of all species was affected by habitat use, while density seems only to be important for selection of blueberry.

4.2.1 Factors describing habitat

The best model including only factors describing habitat features explained 20.5 % of the variation in browsing frequency of rowan, 14.5 % of blueberry variations, and 18.8 % of the variation in birch browsing frequency. Habitat description and habitat productivity seem to be the most important variables of explaining spatial differences in browsing. Browsing of rowan was highest in very high and normal to low productive habitats. Browsing of blueberry was highest in very high productive habitats. Highest browsing of birch was found in high productive areas and the lowest in areas with very high productivity, but this result should be considered with caution since this study did not make any distinctions between birch branches and root shoots. The habitat selection of red deer changes both through the season and within the day, and a study discovered selection for areas of very high and high productivity in the daytime, and some but not so much in the night time in wintertime (Rivrud 2007). The study reported no specific selection or avoidance of average to low productivity. Selection of habitat productivity may explain a part of spatial variations in browsing frequency of blueberry, and may explain some of the variation in rowan, but seem not to do so for birch. Rowan growing in deciduous forest habitats seems to be preferred, while selection of blueberry was highest in deciduous and mixed forests. Habitat description had no important significant effect on the spatial variations of browsing frequency in birch. When excluding birch, a trend of more browsing for vegetation in deciduous forests of very high productivity, elements usually related to high quality ungulate habitats (Hanley 1984, Danell et al. 1991, Jedrzejewska et al. 1994), seems to emerge, but the high levels of browsing on rowan in normal to low productive areas is difficult to explain. High quality habitats may consist of plants of higher forage quality or have a favorable plant composition. Some of the variations in habitat type and productivity may be explained by habitat use, and where density is seen to affect browsing intensity, variations between administrative units can affect the importance of selection due to forest types and habitat productivity. Nevertheless, forest type composition and productivity are probably an important component in understanding the overall browsing intensity of rowan and blueberry in Sogn and Fjordane.

Observations suggest that agricultural areas may be very important for red deer in wintertime (Ahlèn 1965, 1975). Other studies have shown a higher selection for agricultural land and pastures in winter, spring and autumn than in the summertime, probably because of larger differences between quality and quantity of forage in forested areas and arable land in the off-growing season (Rivrud 2007). This reflects a trade-off situation between energetic benefits and safety, since arable land often is often considered more dangerous. Key vegetation resources may draw animals to certain areas, resulting in a higher browsing frequency of less favorable species within these areas (Palmer et al. 2003). By being attracted by arable land, the vegetation near these areas could display a higher degree of utilization by the red deer than areas farther away (tasty neighbors). However, contrary to hypothesis H1, neither the highly selected rowan nor the lower selected blueberry and birch showed a higher browsing pressure in areas near arable land. No significant change in browsing pressure of blueberry and birch could be found with distance from arable land, and browsing pressure of rowan was slightly positive with distance from arable land, suggesting that these areas do not affect browsing selectivity of red deer in winter to any large extent. This may reflect that red deer moving from their day areas further away spend little time close to the agricultural fields before entering these.

Blueberry was more heavily browsed in south facing slopes, and browsing of rowan was lowest on west facing slopes. Browsing of birch was not significantly affected by aspect. Aspect is an important part of the deer habitat (Mysterud et al. 2001a). Selectivity will by a large degree be determined by differences in plant quality and/or thermal benefits. While deer in the summertime may select aspects to prolong their access to high nutritional plants (Mysterud et al. 2001a), south facing slopes are expected to be selected in the wintertime because of a larger degree of incoming solar radiation. A greater level of solar radiation is reported to increase performance of elk (Cook et al. 1998). Areas with favorable elements, such as thermal benefits, are expected to have a higher density and area use. The higher browsing of blueberry on south facing slopes likely reflects differences in red deer habitat use or density, while the lower selection of rowan on west facing slopes can not easily be linked to habitat use or density. Why rowan in west facing slopes is less browsed is unknown. The steepness of the slopes may play a minor role in variation in browsing frequency of rowan, where browsing was slightly negative with increasing steepness of the slopes. Blueberry and birch did not change significantly with increasing steepness.

Cover can often be of great importance in selecting a preferable habitat, and may not only hide the animal from potential predators, but will in many instances work as a climate and/or thermal protection, and as an interception cover from rain and snow (Mysterud and Østbye 1999). Areas that intercept snow, like dens spruce forests, may be very important winter habitat for the Scandinavian red deer (Ahlèn 1965). However, no correlation could be found between cover and spatial variation in browsing of rowan, blueberry or birch, suggesting that cover do not play an important role in the red deer's choice of feeding places in wintertime. Cover may be of greater importance in summertime than in the wintertime (Rivrud 2007).

The browsing of rowan and blueberry did not change significantly with altitude. There was a weak, but significant, negative effect by altitude on browsing of birch. Variation in altitude is known to affect the body weight of red deer (Albon and Langvatn 1992, Mysterud et al. 2001a), but have been connected to differences in plant phenology. Lower snow depth in low altitude areas means lower energy expenditure of moving and foraging, and the somewhat higher selection of birch in lower altitudes may reflect a slightly higher use of these areas by red deer. More likely, differences in altitude may be a function of the locality of birch without root shoots (mainly smaller and closely gathered specimens) and birch with root shoots (larger specimens), i.e. spatial differences in forage quality.

4.2.2 Administrative units

The best model including only administrative units explained 11.0 % of the variation in browsing pressure of rowan, 21.1 % of blueberry, and 28.8 % of the variation in browsing frequency of birch. By linking spatial variation in browsing in administrative units to the number of deer shot in these areas, we can estimate the density effects on browsing pressure and diet selection. Competition for food increases at high densities in the winter (Albon et al. 1983), and the selectivity of the herbivores will be reduced (Mysterud 2006). Studies have shown ungulates to eat more low quality food in high density populations (Freeland and Choquenot 1990), and studies in Scotland have shown that the competition for food increases at high densities in the winter (Albon et al. 1983). I expected that highly palatable species would be browsed irrespective of density. The highly palatable rowan showed little variation in browsing levels between administrative units, as predicted from hypothesis H2A. Both blueberry and birch showed spatial variation between administrative units, which can depending on size arise both due to differences in habitat use and effects of density variations. As predicted from H2B, browsing of blueberry showed clear correlation with density of red deer, confirming that browsing of this intermediate forage quality is at least partly density dependent. Some of the variations in browsing frequency on blueberry between administrative areas may be due to habitat differences. Browsing frequency on birch was not affected by density of red deer, suggesting that the spatial differences in browsing may be due to habitat use. Another possibility is that the root shoots of birch is highly selected, and that the lack of density dependence for birch is due to high utilization of these plant parts. The low browsing levels observed for birch (compared to the expected values of a highly selected species), may be because this study made no distinctions between browsed root shoots and branches, and that the browsing frequency of the branches weigh down the overall browsing frequency of birch. The spatial differences observed in productivity and administrative units will then perhaps be a function of spatial differences in forage quality. The majority of birch root shoots were found in blocks located within the municipality of Flora, where selection of birch happens to be generally higher. This may explain some of the altitudinal differences in birch selection, since Gloppen is generally higher above sea level than Flora. The browsing level of all three study species showed positive correlation with faeces counts, suggesting as expected that browsing frequency is clearly influenced by habitat use. It is likely that some of the selectivity variations in different factors describing habitat are simply due to differences in area use.

4.3 To what extent can browsing inventories help management?

Many wildlife managers focus on animal population size when assessing the impacts of herbivores on the ecosystem. The most sensitive parameter to respond to changes in population density is early growth, which affect the time of first reproduction, and fecundity of young females (Gaillard et al. 2000, Mysterud 2006). This can easily be measured by body weight alone, or other anatomical variations like jaw or foot length, on animals shot by hunters. Strong evidence of linearity between density and body weight have been reported for red deer in Norway (Mysterud et al. 2001b), while the relationship is non-linear for female fecundity (Langvatn et al. 2004). However, the population size itself will not give us information about the state of interactions between the population and its surrounding ecosystem (Morellet et al. 2007). As a population of herbivores grows, measurable effects on the plant community are likely to increase, and monitoring of the plant community may give us an indication of the herbivore status after a population increase. In theory, effects of density increase can be observed on the plant community before any effects will be seen on the animals (Noy-Meir 1975). Unless it is highly tolerant, highly selected species is first to respond to effects of grazing, and a decrease in abundance will be almost directly connected to overgrazing (Mysterud 2006). This will, however, depend heavily on the vegetation composition in the ecosystem (Mysterud 2006). The idea of using ecological indicators to monitor populations of large herbivores is rooted in the concept of density dependence (Morellet et al. 2007), and may be a very useful tool in herbivore management. Dale and Beyeler (2001) argued in a recent review that an ecological indicator 'should be easily measured, be sensitive to stresses on the system, respond to stress in a predictable manner, be anticipatory, predict changes that can be averted by management actions, be integrative, have a known response to disturbances, anthropogenic stresses, and changes over time, and have low variability in response'. This, however, is a goal that very often is extremely difficult to achieve.

When animals are feeding on plants, a cascade of effects is likely to arise in the plant community. To counter herbivory, a plant can either try to tolerate the damage that has been caused to it (plant tolerance), or avoid herbivory altogether by mechanical, structural or chemical defenses (plant resistance). Plants differ in their tolerance and resistance to herbivores. The characterization of a plant with high tolerance may be increased photosynthetic rate and/or branching after damage to the plant, high relative growth rate, low access to growth tissue, high root-to-shoot ratio, a tufted or matlike growth form, high levels of carbon storage in the root and/or the ability to allocate carbon storage from root to shoots after damage (Strauss and Agrawal 1999, Mysterud 2006). Timing of herbivory relative to the growing season and the length between herbivore damage factors can also affect the tolerance of a plant (Augustine and McNaughton 1998), and so can different environmental factors (Strauss and Agrawal 1999). Studies have shown that selective feeding by ungulates can both increase and decrease the abundance of palatable and unpalatable plant species, depending on location, grazing intensity, ecological history and environmental relations (Augustine and McNaughton 1998). Nevertheless, beyond a certain point of grazing intensity, species are most likely to be suppressed if the grazing pressure is not reduced. Selective feeding of seedlings may effectively alter the appearance of a forest (Augustine and McNaughton 1998).

It is yet difficult to determine whether the reported browsing frequency in Sogn and Fjordane have had a measurable effect on the plant community, since little is known about our ecosystems regarding how much stress the plants can cope with. A North American review of grass dominated ecosystems concluded, that on average heavy grazing (desirable species do not maintain themselves) was 57% utilization of primary forage plants, moderate grazing (desirable species can maintain themselves, but do not improve production) was 43%, and light grazing was 32% utilization (desirable species maximize their herbage producing ability) (Holechek et al. 1999). In municipal Gloppen, 56 % of the available browse (twigs under two m) of rowan, 33 % of blueberry and 17 % of birch have been browsed the latter years. In the municipality of Flora, 61 % of rowan, 22 % of blueberry and 40 % of the available birch have been browsed. The rowan is thus approaching a heavy browsing pressure in both Gloppen and Flora. It is therefore valid to ask whether this species will soon be, or may have been for a while, decreasing in abundance in this areas. It is difficult to say something conclusive about browsing intensity of birch, but the branches are probably very lightly browsed, while the root shoots are moderate to heavy browsed. The blueberry is more unevenly browsed in Flora and Gloppen, reflecting an overall lower selectivity, but some high density areas may be highly browsed. Earlier studies on the west coast of Norway concluded that browsing by red deer has a strong, negative influence on blueberry size, abundance and fruit set (Hegland et al. 2005). Controlled clipping experiments showed that blueberry may need more than five years to totally recover from severe clipping (Tolvanen et al. 1994). The clear density effect tells us that the browsing pressure of blueberry is not only determined by habitat quality or spatial interspecies differences, but that differences in red deer density between local areas determine how much the blueberry are browsed. Further studies should investigate whether blueberry browsing have any effect on animal traits that are expected to be affected by overabundance, which may be a useful tool in red deer management in Sogn and Fjordane.

5 Conclusion

Among factors affecting red deer browsing pressure, we have from this study learned that habitat forest description and productivity are among the most important, even for highly selected species like rowan. Although many red deer managers emphasize the importance of population densities, density by itself will not give us any information of how the late increase red deer populations is affecting the plant community (Morellet et al. 2007). This study documents that many plant species in Sogn and Fjordane are at present highly browsed. It is therefore relevant to conduct further studies aimed at learning whether changes in plant community structure have occurred the last decades. Blueberry may be a useful tool as an ecological indicator in red deer management in Sogn and Fjordane. It is considered a key species in many Norwegian forests, is abundant in Sogn and Fjordane, and the response to stresses are fairly well known. Browsing pressure of blueberry is seen not only to be determined by biological factors describing the habitat or spatial interspecies differences, but browsing levels are also related to local differences in red deer density. Availability does not affect browsing pressure of blueberry to any large degree. The next logic step for future investigations will be to link local browsing pressure of plants affected by red deer density with other ecosystem factors that may be affected by oversized populations. This way we may get an insight of how the plant community interacts with the red deer population enabling sustainable management.

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Appendices

Appendix 1. Set up of administrative units

Table A1. The table shows how the administrative units in this paper are connected. Four administrative levels were used; county (n=1), municipal (n=2), block (n=6) and hunting area (n=23).

County	Municipal	Block	Hunting area
Sogn and Fjordane	Flora	Eikefjorden	*Eikefjord storvald
			Endestad
			*Norddalsfjord storvald
		Norddalsfjorden	Midtbø
			*Norddalsfjord storvald
			Strømsnes
			Terdal/Klauene
		Sunnfjord	*Eikefjord storvald
			Skålefjell Hjortevald
			Stavøy
			Steindal, Svartdal, Osen
			Vasset ytre
	Gloppen	Breim	*Blåfjellet Driftsplanområde
			Dale og Kåle
			Gloppen Sør Viltlag
			Hetle - Reed - Fløtre
		Byrkjelo	*Blåfjellet Driftsplanområde
			Fossheim, Sandal og Torheim
			Hole, Moldestad og Felde
			Kleppe, Støyva og Bjørnereim
			Myklebust, Kobberstad
			Øvreset
		Hyen	Gjengedal
			Mjellem
			Ommedal
			Vestre Hyen storvald

* The same Hunting area exists in more than one block.

Appendix 2. Study species

Table A2. Summary of which specimens within the 4 m radius measuring plots that was measured.

Specie	Measured
Blueberry	All within the 50x50 cm frame
Birch	The nearest tree to the middle
Cowberry	All within the 50x50 cm frame
Heather	The nearest tree to the middle
Rowan	All trees within the plot
Pine	All trees within the plot
Alder	The nearest tree to the middle
Bird cherry	The nearest tree to the middle
Sallow	All trees within the plot
Other willow	All trees within the plot
Hazel	The nearest tree to the middle
Moorberry	All within the 50x50 cm frame
Oak	The nearest tree to the middle
Spruce	All trees within the plot
Aspen	All trees within the plot
Holly	The nearest tree to the middle

Appendix 3. Field tables.

Two separate work-tables were used at the field work. The tables focus mainly on either species of trees or heath. Both tables were used at every measuring plot.

Table A3. This table used in the field focuses on browsing frequency and general appearance of trees, as well as faeces counts, habitat description, dominant tree height, and canopy cover.

Date		Block						Species=Trees							
GPSno=plot no		Each plot has a 4m radius							dbh= diameter breast height						
Grazing 0-200 cm		One line per individual tree		Canopy cover							Twigs	Grazed	Grazed		Bark
GPSno	Faeces	Habitat	Dom tree height	N	E	S	W	Species	dbh	Height (cm)	Total no	Fresh	Old	Ungrazed	Gnawing

Table A4. This table used in the field focuses on browsing frequency, general appearance and growth of heath, as well as slope and aspect.

Date		Block				Species=Heath								
GPSno=plot no														
Grazing 0-200 cm		field-0.5x0.5 m square								Twigs	Grazed	Grazed		Bark
GPSno				Slope	Aspect	Species	Distance	Coverage (%)	Height	Total no	Fresh	Old	Ungrazed	Gnawing

Appendix 4. Model selection

Separately models were carried out for rowan, blueberry and birch. The model selection was based on the AIC criterion, and was analyzed at three different levels; (1) administrative units, (2) factors describing habitat and (3) factors indicating red deer density and use. The best model is given the AIC value “0”.

Table A5. Model selection of rowan. Hunting area was excluded from the model selection of rowan at the administrative level.

Rowan	Municipality	Block	Hunting area	Aspect	Habitat	Productivity	Distance to arable land	Distance to coast	Cover	Slope	Altitude	Density	Area use	AIC
1. Administration	x													23.54
		x												0
			--											
2. Factors describing habitat				x	x	x	x	x	x	x	x			2.322
				x	x	x	x	x	x	x				0.676
				x	x	x	x	x	x					3.173
				x	x	x	x	x		x				2.023
				x	x	x	x		x	x				0
				x	x	x			x	x				1.398
				x	x		x		x	x				5.498
				x		x	x		x	x				0.255
					x	x	x		x	x				16.568
				x	x	x	x		x					2.735
				x	x	x	x			x				0.555
3. Density and use												x	x	0.4469
												x		15.318
													x	0

Table A6. Model selection of blueberry.

Blueberry	Municipality	Block	Hunting area	Aspect	Habitat	Productivity	Distance to arable land	Distance to coast	Cover	Slope	Altitude	Density	Area use	AIC
1. Administration	x													42.444
		x												39.556
			x											0
2. Factors describing habitat				x	x	x	x	x	x	x	x			7.153
				x	x	x	x	x	x	x				5.161
				x	x	x	x	x	x					4.016
				x	x	x	x	x						2.884
				x	x	x	x							1.694
				x	x	x								0
				x	x									2.390
				x		x								17.943
					x	x								1.515
				x	x	x		x						1.147
				x	x	x		x	x					2.276
				x	x	x		x		x				2.688
				x	x	x		x			x			3.147
3. Density and use												x	x	0
												x		3.5645
													x	12.891

Table A7. Model selection of birch.

Birch	Municipality	Block	Hunting area	Aspect	Habitat	Productivity	Distance to arable land	Distance to coast	Cover	Slope	Altitude	Density	Area use	AIC
1. Administration	x													3.139
		x												0
			x											4.829
2. Factors describing habitat				x	x	x	x	x	x	x	x			8.206
				x	x	x	x	x	x	x				12.799
				x	x	x	x	x	x		x			6.375
				x	x	x	x	x			x			7.309
				x	x	x	x		x		x			5.445
				x	x	x			x		x			4.931
				x	x				x		x			9.894
				x		x			x		x			4.487
						x			x		x			0.512
					x	x			x		x			1.642
						x	x		x		x			0.875
						x		x	x		x			1.611
						x			x	x	x			2.277
						x			x					22.498
						x					x			0
3. Density and use												x	x	1.9776
												x		4.3559
													x	0

Appendix 5. Availability.

Table A8. Availability of rowan, blueberry and birch brows in the six administrative units "block", based on in how many plots specimens are to be found relative to the total number of plots in the block.

Specie	Breim	Byrkjelo	Hyen	Eike-fjorden	Norddals-fjorden	Sunnfjord
Rowan	5.1 %	21.6 %	12.4 %	28.8 %	34.8%	20.2 %
Blueberry	74.6 %	78.4 %	78.4 %	79.8 %	78.7 %	77.1 %
Birch	39.0 %	63.5 %	43.3 %	35.6 %	46.1 %	22.0 %